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Setting an ecological baseline prior to the bottom-up establishment of a marine protected area in Santorini Island, Aegean Sea

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Abstract

Since 2010, a bottom-up initiative has been launched in Santorini Island (Aegean Sea, Eastern Mediterranean) for the establishment of the first fully protected marine protected area in the Cyclades, aiming at improving fisheries and enhancing responsible recreational uses at sea. Following discussions with local small-scale fishermen and divers, two sites along the southern and south-eastern coasts of the island were suggested as suitable to this end. In 2012, a baseline study was conducted in these areas to assess their state and provide an ecological snapshot that would enable sound designation and monitoring. Several *ad hoc* indices and metrics were applied, taking into account structural and functional features of the upper infralittoral algae and *Posidonia oceanica* seagrass beds. An integrated assessment of the infralittoral fish assemblages and their associated benthic communities was also performed. Our most important findings were: (i) the low total fish biomass and the absence of adult top predators, indicating overfishing; (ii) the overgrazing effects of the abundant alien herbivore spinefoot fishes (*Siganus* spp.), as reflected by the abnormal structure of the algal communities; (iii) the scarcity of indications of pollution or other direct anthropogenic pressures, as indicated by the good environmental status of the *P. oceanica* meadows and the upper infralittoral vegetation; and (iv) the presence of a rich diversity of species and habitats, especially along the Akrotiri Peninsula and the wider volcanic Caldera. These findings provide useful insights on the strengths and weaknesses of the study area and are discussed together with their implications for protection and management.

Keywords: Marine protected area, fish assemblages, benthic communities, rocky infralittoral, *Posidonia oceanica* meadows, ecological indicators, Aegean Sea, alien species.

Introduction

Historical and current overfishing in synergy with multiple other anthropogenic pressures, such as urban pollution and agricultural runoff, has led to the degradation of marine ecosystems across the Mediterranean Sea (Bianchi *et al.*, 2012; Micheli *et al.*, 2013). This situation is increasingly evident in the typically oligotrophic waters of the Eastern basin and particularly in the marine area of the Cyclades (Stergiou, 2002; Pennewiss, 2004; Giakoumi *et al.*, 2012). Declines in fishery resources profoundly affect local fishers but also marine-based tourism, such as SCUBA diving and snorkelling activities that are driven by a strong interest in marine wildlife observation (PISCO & UNS, 2016).

One practical solution to improve local fisheries and promote responsible tourism whilst enhancing nature conservation is the creation of marine protected areas (MPAs). When considering MPAs in either theory or practice, however, a wide variety of concepts and definitions may apply, encompassing practically everything from

marine parks established for the protection of threatened or unique species and habitats, vast areas with various levels of protection, or even sites of historical or cultural interest (Agardy, 2000). According to Lubchenco and Grorud-Colvert (2015), MPAs can be distinguished into: lightly protected, where some protection exists but significant extractive activity is allowed; strongly protected, where all commercial activity is prohibited, and only light recreational and subsistence fishing is allowed; and fully protected, also known as "marine reserves" or "notake zones", where no extractive activities are allowed. Commonly, the primary goal of MPAs is the conservation of marine biodiversity and ecosystems; however, social, economic, and cultural goals can also be central in their designation (Day *et al.*, 2012).

A global review synthesizing evidence on the effects of fully protected MPAs across the globe demonstrated that MPAs can contribute to an average increase of 21% in species diversity, 28% in the size of organisms (algae, invertebrate and fish species), 166% in density (number of individuals per unit area), and 446% in biomass (kg per

hectare), compared to adjacent unprotected areas (Lester *et al.*, 2009). These percentages, however, refer only to fully protected MPAs where no fishing or other extractive uses are allowed within their boundaries. A necessary prerequisite to detect such positive effects is the successful enforcement and compliance with the rules set within an MPA. When this prerequisite is not met, the MPA effects are substantially reduced or negligible (e.g. Montefalcone *et al.*, 2009; Campbell *et al.*, 2012; Sala *et al.*, 2012; Guidetti *et al.*, 2014).

Up to 2015, more than 1,100 marine areas have been designated as MPAs across the Mediterranean Sea, corresponding to a total area of about 163,000 km² or 6.5% of the basin's surface (PISCO & UNS, 2016). These designations refer to all MPA categories, including the large Pelagos Sanctuary and Natura 2000 marine sites, many of which still lack management plans and authorities. Fully protected marine areas are estimated to barely cover 0.04% of the Mediterranean Sea (PISCO & UNS, 2016). In reality, this percentage is even smaller, considering that even in many fully protected areas of the Mediterranean poaching and other illegal destructive activities still occur (Guidetti *et al.*, 2008; Sala *et al.*, 2012).

Limited funding allocated to nature conservation and enforcement of MPA management measures in most Mediterranean countries (Katsanevakis et al., 2015) can partly explain the high occurrence of poaching in Mediterranean MPAs. In addition, low compliance with the rules of MPAs by local communities might be attributed to the low level of stakeholder engagement in the planning and management process. Traditionally, nature conservation has been a top-down procedure at either national or regional scale. There is now growing consensus among scientists that bottom-up approaches, i.e. involving stakeholders and local communities at an early stage of MPA establishment, is necessary to achieve social acceptance and compliance. These factors can prove to be more crucial for determining the success of an MPA than design factors, e.g. the size of the MPA (Pollnac et al., 2010; Daw et al., 2011; Campbell et al., 2012; Ferreira et al., 2015). In the Mediterranean Sea, there are few cases where stakeholders have been actively involved in MPA planning since the onset of the initiative. Such successful examples are the Marine Park of Côte Bleue in France (Claudet et al., 2006; Leleu et al., 2012) and the Torre Guaceto MPA in Italy (Guidetti et al., 2010), where increased social support and enhanced MPA positive effects have been demonstrated. In light of this evidence, a bottom-up initiative was launched in Santorini Island (Aegean Sea, Eastern Mediterranean) aiming at improving fisheries and enhancing the recreational uses of the area.

At global scale, Santorini is considered an island of unparalleled beauty. More than 500,000 tourists per year visit the island to enjoy its breath-taking volcanic sceneries. This tourism flow, however, has been stretching the island's limits beyond sustainable levels, thus threatening

its unique culture and environment (Wadih, 2005). New tourism development paradigms are therefore needed, and in particular such that seek to eliminate negative tourism impacts, preserve and capitalize on the natural and cultural local resources, and maximize benefits for local communities and stakeholders. The ongoing initiative focused on building consensus among small-scale fishers, recreational diving centres, local authorities and the general public for the creation of the first fully protected area in the Cyclades Islands, Aegean Sea (Cousteau *et al.*, 2010). Following lengthy discussions, two coastal areas of relevant interest were eventually suggested as suitable MPA candidates.

A baseline study was then conducted to assess the natural state of these two areas, according to ecological and environmental criteria. Establishing ecological baselines prior to protection has been a major challenge in marine conservation, given that assessment of the status of coastal ecosystems before the implementation of management schemes has seldom been applied in existing MPAs worldwide (Jennings, 2000; Willis *et al.*, 2003; but see Osenberg *et al.*, 2011 for exceptions). Therefore, the scope of our sampling design was to obtain meaningful qualitative and quantitative information on the current ecological state and future potential of the candidate sites. Such information can prove valuable in providing rigid "ecological snapshots" that enable sound MPA designation and allow for future monitoring of management effectiveness.

Materials and Methods

Study area and sampling design

The volcanic Santorini Island complex includes the islands of Thera, Therasia, Nea Kameni, Palia Kameni, and Aspronisi. They all represent the remains of the collapsed volcanic shield and form a ring around a large submarine caldera that was formed around 1600 BC (Nomikou *et al.*, 2014). The study area comprises two main sub-areas along the coasts of Thera Island: Perissa Rock (PR), encompassing a rocky coastline of approximately 2.5 km on the south-eastern coast of Thera Island, between the sandy beaches of Perissa and Kamari villages; and the Akrotiri Peninsula (AK), a 6.5 km coastline stretching along the south-western part of Thera Island (Fig. 1).

A total of 18 sites were surveyed including 4 sites along Perissa Rock (PR-1, PR-2, PR-3 and PR-4), 7 sites along Akrotiri Peninsula (AK-1, AK-2, AK-3, AK-4, AK-5, AK-6 and AK-7), and 7 control sites selected beyond the boundaries of the proposed areas (CT-1 at Megalochori, PK-1 and PK-2 at Palia Kameni, NK-1 at Nea Kameni, AN-1 and AN-2 at Aspronisi) (Fig. 1).

Site selection was based on a systematic random scheme, placed 1 km apart in the case of Akrotiri Peninsula, and 750 m apart in the case of Perissa Rock. Given the specific requirements of the study in terms of suitable depths and habitats, the final site position had at times to

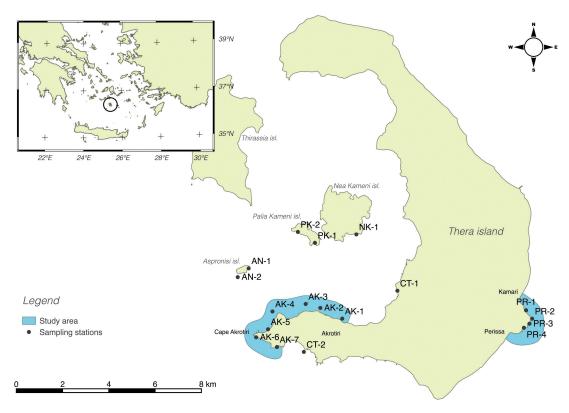


Fig. 1: Map indicating stations along the coasts of Perissa Rock (PR) and Akrotiri Peninsula (AK) (shaded polygons), and several scattered control sites (CT-1, CT-2, NK-1, PK-1, PK-2, AN-1, AN-2).

be slightly readjusted on the spot to ensure habitat presence and continuity.

We focused our research on infralittoral rocky reefs and Posidonia oceanica seagrass meadows (Habitat Types 1170 and 1120 respectively, sensu the EU Habitats Directive 92/43/EEC), as these habitats support the highest fish biomass in the Mediterranean (Harmelin-Vivien et al., 2005; La Mesa et al., 2011; Giakoumi & Kokkoris, 2013) and provide a wide array of marine ecosystem services (Salomidi et al., 2012). To assess the ecological status of these habitats, ad hoc indices and metrics were applied (Orfanidis et al., 2001; Boudouresque et al., 2006; Montefalcone et al., 2007), along the lines of the Habitats (92/43/EEC) and Water Framework (WFD, 2000/60/EE) EU Directives, taking into account the morphological, structural and life-history features of the habitat-forming macrophytes (macroalgae and *P. oceanica*). Furthermore, an integrated assessment was performed at 5 and 15 m depth, jointly addressing structural aspects of fish assemblages and their associated benthic communities (e.g. Sala et al., 2012).

Fieldwork protocols and data analysis

Ecological status assessment

A. Shallow rocky reefs

The Rapid Assessment of Coastal Ecological Status (RACES) methodology was applied to assess the eco-

logical quality status (sensu the WFD) of shallow rocky reefs; this methodology consists in the application of the Ecological Evaluation Index (EEI) (Orfanidis et al., 2001) on photographic samples of macroalgae along the upper infralittoral zone (0-1 m) (Salomidi, 2009). At each site, six systematic randomly placed photoquadrats (21 cm × 30 cm) were obtained at equal distances along a 25 m transect line and the images were analysed at the laboratory. Conspicuous species were identified to the lowest possible taxonomic level or morphological group, and mean percentage cover per species (or higher taxon) was estimated using a superimposed digital grid in the Adobe Photoshop CS5 image editing environment. All taxa identified were assigned to Ecological State Group (ESG) I or II, as defined by their morphological, life-history and ecophysiological traits; the Ecological Evaluation Index (EEI), designed to reflect the macroalgal communities response to varying levels of nutrient enrichment in a water body, was subsequently applied to allow the classification of each site among five distinct Ecological Status categories (i.e. bad = 2, low = 4, moderate = 6, good = 8, and high = 10) (Orfanidis et al., 2001).

B. Posidonia oceanica meadows

To assess the ecological quality status and the vitality of *P. oceanica* meadows, a set of key structural and functional metrics was considered, namely: meadow cover (%), shoot density (shoots m⁻²), plagiotropic growth of

rhizomes (%), and meadow lower limit typology (Appendix, Table 1). Each of these metrics provides useful information on the vitality of the P. oceanica meadows for a wide spectrum of anthropogenic disturbances (i.e. nutrient enrichment, sediment resuspension and turbidity, mechanical disturbance) (Pergent-Martini et al., 2005). With the exception of the meadow lower limit typology, all other metrics were sampled at a standard depth of 15 m to prevent the masking effects of depth variability (Alcoverro et al., 1995). Table 1 of the Appendix summarizes all metrics considered along with their anticipated responses to different impacts, and outlines their respective methodological protocols. The interpretation of the estimated values for each metric is based on the standardized scales summarized in Table 2 of the Appendix (Pergent et al., 1995; Boudouresque et al., 2006; Montefalcone, 2009; UNEP/MAP-RAC/SPA, 2011; Pergent et al., 2015).

Integrated assessment of fish and benthic assemblages

A. Infralittoral fish communities

To survey infralittoral fish communities at each site, visual censuses were performed along three replicate 25 m × 5 m transect lines, at 5 m and 15 m depth, where either rocky reefs or *P. oceanica* meadows occurred. The diver conducting the fish survey moved at a constant speed identifying, counting, and attributing all individuals to 5 cm size classes within 2.5 m on either side of the transect lines (La Mesa & Vacchi, 1999). Length estimates of fish counted during the surveys were converted to wet weight by using the allometric length–weight conversion formula: $W = a L^b$, where W is the weight in grams and L is the total length in cm. Parameters a and b are constants obtained from Giakoumi et al. (2012) and Fishbase (www.fishbase.org). Where values for a and b were not available, the parameters from congeneric species with similar shape and maximum total length were used. We chose the parameter values that best corresponded

Table 1. Station code name and location, coordinates in decimal degree format (WGS '84 Datum) and description of the occurring habitat types.

Name	Location	LAT	LON	Depth(m)	Habitat types
AK-1	Akrotiri	36.36345	25.39550	5	Posidonia bed
AK-I	Peninsula	30.30343	23.39330	15	Vertical rocky wall
AK-2	Akrotiri	36.36774	25.38503	5	Posidonia bed
AK-Z	Peninsula	30.30774	23.36303	15	Posidonia bed
AK-3	Akrotiri	36.36935	25.37799	5	Vertical rocky wall
AK-3	Peninsula	30.30933	23.31199	15	Vertical rocky wall
AK-4	Akrotiri	36.36663	25.36195	5	Horizontal continuous rock
AN-4	Peninsula	30.30003	25.30193	15	Vertical rocky wall
AK-5	Akrotiri	36.35971	25.35969	5	Horizontal continuous rock
AK-3	Peninsula	30.33971	23.33909	15	Posidonia bed
AK-6	Akrotiri	36.35665	25.35392	5	Horizontal continuous rock
AK-0	Peninsula	30.33003	23.33392	15	Posidonia bed
AK-7	Akrotiri	36.35275	25.36387	5	Vertical wall
AK-/	Peninsula	30.33273	23.30387	15	Posidonia patches on sandy bottom
				5	Horizontal continuous rock with medium
AN-1	Aspronisi	36.38355	25.35078	3	boulders
				15	Vertical rocky wall
AN-2	Aspronisi	36.38018	25.34545	5	Horizontal continuous rock with crevices
AIN-Z	Aspromsi	36.37772	25.34442	15	Posidonia bed
CT-1	Magalaghari	36.37400	25.42227	5	Posidonia bed with medium boulders
C1-1	Megalochori	30.3/400	23.42227	15	Posidonia bed
CT-2	Akrotiri	26.25070	25 27(79	5	Medium boulders
C1-2	Peninsula	36.35070	25.37678	15	Posidonia beds
NK-1	Nea Kameni	26 20610	25 40200	5	Large boulders
INK-I	Nea Kameni	36.39618	25.40289	15	Large boulders
PK-1	Palia Kameni	36.39310	25 20200	5	Large boulders
PK-I	Pana Kamem	30.39310	25.38290	15	Vertical rocky wall
PK-2	Palia Kameni	36.39746	25 27472	5	Large boulders
PK-2	Pana Kamem	30.39/40	25.37473	15	Large boulders
PR-1	Perissa Rock	36.36563	25.48410	5	Sub-horizontal wall
DD 2	D : D 1	36.36232	25.48697	5	Vertical rocky wall
PR-2	Perissa Rock	36.36157	25.48739	15	Sandy with <i>Posidonia</i> patches
PR-3	Perissa Rock	36.36038	25.48563	7-9	Horizontal continuous rock with small boulders
PP 4		36.35883	25.48294	5	Vertical rocky wall
PR-4	Perissa Rock	36.35601	25.48396	15	Sandy with large <i>Posidonia</i> patches

Table 2. Vitality of *Posidonia oceanica* meadows. Mean values (\pm SE) of each metric per sampling site.

Sampling Site	Lower Limit type	Meadow Cover (%)	Conservation Index (CI)	Shoot density (shoots m ⁻²)	Plagiotropic growth of rhizomes (%)	Synthesis (Mean metric values)
AK-2	Erosive	92.0 ± 6.1	0.97 ± 0.01	289.6 ± 41.3	27.2 ± 6.8	4.0 (<i>good</i>)
AK-5	Erosive	55.3 ± 5.9	0.82 ± 0.38	514.6 ± 33.1	12.0 ± 2.1	4.2 (<i>good</i>)
AK-6	Progressive	68.4 ± 6.2	0.81 ± 0.11	418.7 ± 19.9	15.5 ± 3.4	4.0 (good)
AN-2	Progressive	64.8 ± 5.1	0.94 ± 0.03	637.5 ± 40.3	12.7 ± 2.5	4.5 (good)
CT-1	Erosive	95.6 ± 4.4	0.96 ± 0.04	310.4 ± 43.6	11.8 ± 4.5	4.0 (good)
CT-2	Progressive	71.3 ± 3.2	0.93 ± 0.04	581.3 ± 30.3	12.3 ± 1.1	4.5 (good)
PR-2	Progressive	71.2 ± 3.3	0.93 ± 0.04	364.6 ± 29.7	27.3 ± 7.0	4.0 (good)
PR-4	Progressive	41.2 ± 12.5	0.86 ± 0.08	404.3 ± 67.1	34.5 ± 8.7	3.7 (<i>good</i>)

to our study area (Cyclades Islands), or the closest geographical area available (usually located in the Eastern Mediterranean). Fish taxa were assigned to functional groups based on published diet and trophic level data (www.fishbase.org), i.e. zooplanktivores, herbivores, carnivores and apex predators (Guidetti & Sala, 2007; Giakoumi & Kokkoris, 2013).

B. Structure and composition of benthic communities

The composition and structure of benthic communities were studied within 12 replicate quadrats (20 cm × 20 cm) randomly placed along each 5 m and 15 m transect line, provided that rocky substrata occurred at these depths. For each quadrat, the percentage cover (%) of the different benthic components was estimated in situ, and classified into distinct layers (Sala et al., 2012), namely the canopy (large-sized perennial slow-growing algae, i.e. Cystoseira, Sargassum), the bushy (fleshy medium-sized algae that typically occupy the open space between and underneath the canopy, e.g. Padina, Dictyota, Halopteris, Gelidium), the calcified (including both erect, e.g. Amphiroa, Jania, and encrusting corallines, e.g. Lithophyllum, Mesophyllum), the turf (consisting of minute, typically seasonal and fast growing species, e.g. Sphacelaria, Cladophora, Bryopsis, also including cyanophyte and chrysophyte mats), and the epiphyte layer (comprising minute seasonal species, e.g. Ceramium, Dasya, Herposiphonia, growing on larger algal thalli). Benthic invertebrates and bare rock, identified as rocky substratum deprived of any marine macrobiota, were also recorded and treated as separate layers in the analyses.

C. Sea urchin biomass

Sea urchin size and density were recorded using 50 cm × 50 cm quadrat frames placed randomly along the 5 m and 15 m transect lines. A total of 12 quadrats (4 per transect), i.e. an area of 3 m² were sampled per depth at each site. The size of each individual (>1 cm test diameter without spines) was measured *in situ* using calipers. Sea urchins were grouped into 1 cm size classes (Sala & Zabala, 1996) in order to examine the size-frequency

distribution of their populations. Biomass was estimated based on the size-weight relationships provided by a previous study conducted in the same region (Giakoumi *et al.*, 2012).

Other species of interest

At all sites and transect lines surveyed, the presence of conspicuous species, with special emphasis on species of conservation interest and alien species, was recorded *in situ* upon detection. For the list of benthic invertebrates of special conservation interest, all relevant national laws and Annexes of the EU directives and international agreements were considered, namely the Greek Presidential Decrees 67/1981; 227/200; 109/2002; The Red List of IUCN; The Red Book of Threatened Animals of Greece, 2009; Habitats Directive 92/43/EEC; The Bern Convention, 1979; The Protocol of Barcelona Convention, 1995; and the CITES Convention, 1973.

Statistical Analyses

Differences between sampling sites were tested using One-way ANOVA for independent samples when conditions of normality and homogeneity of distribution were met; if not, the non-parametric Kruskal-Wallis H-test was applied. Normality of distribution was investigated using the Shapiro-Wilk normality test and homogeneity of variance using Levene's test. Correlations among variables were tested using Spearman's rank correlation coefficient. All differences were considered significant at p < 0.05. Similarity percentage analysis (SIMPER) was performed to detect and express dissimilarities in benthic community layers between stations using the unprocessed algal data set.

Data analyses were performed using the IBM SSPS Statistics 20, STATISTICA StatSoft™ v.6, R Core Team (2016), and PRIMER v.6.1.8 software packages.

Results

Of all sites inspected, continuous horizontal rocky substratum was the most widespread habitat type at both survey depths, i.e. 5 m and 15 m (Table 1). *P. oceanica* meadows were also common, especially at 15 m depth. Sandy bottoms, gravel and boulders were ubiquitous across the study area, while coralligenous assemblages, drop-offs and overhangs were particularly common along the steep-sloping Caldera coasts.

Ecological status assessment

A. Shallow rocky reefs

Out of a total of 108 photoguadrat samples, 19 phytobenthic taxa were identified, among which 7 down to species level, 6 to genus level and the rest within higher taxonomic or morphological groups (e.g. Laurencia spp. complex, filamentous turf, encrusting red algae). Thick leathery perennial species of Cystoseira were dominant almost throughout the upper infralittoral zone of the study area (mean cover \pm SE: $42.8 \pm 4.8\%$), followed by turf algae (including various filamentous opportunistic families, e.g. Cladophorales, Ceramiales, Sphacelariales) (20 \pm 2.8%), erect calcified species of *Jania* (18.8 \pm 2.3%), and various encrusting red algae such as the crustose perennial *Lithophyllum* spp. $(6.9 \pm 1.6\%)$. The alien Caulerpa cylindracea was only detected in low cover $(0.1 \pm 0.09\%)$. A list of all taxa identified, their mean cover values \pm SE across sites and their respective ESG category, is given in Table 3 of the Appendix.

According to the SIMPER analysis, most sites presented a high level of similarity (71.4%) for which *Cystoseira* spp., *Jania* spp. and turf algae were identified as the main contributing taxa (55.3%, 20.5% and 17.3% respectively). Only stations NK-1 (Nea Kameni Islet) and PR-1 (Perissa Rock, north) showed significant dissimilarity (*Kruskal-Wallis test, p* < 0.005), mostly due to the scarcity of *Cystoseira* spp. (contributing by 34.9%) and the relatively increased local dominance of the *Laurencia* species complex, turf algae, *Sargassum* spp., and *Jania* spp. (contributing 19.5%, 13.9%, 12.9%, and 10.4% respectively).

The application of the EEI index classified most sites within *good* or *high* ecological status, but stations AK2 and AK6 were evaluated as *moderate*, and station NK-1

as bad (Fig. 2). The mean EEI numerical value calculated for the whole study area was 8.8 ± 2.18 , reaching up to 9.2 ± 1.42 if the highly disturbed NK-1 station is excluded. These values correspond to a good to high ecological status largely characterizing the upper infralittoral rocky shores (83.3% of the studied stations), both within and outside the sheltered Caldera region.

B. Posidonia oceanica meadows

Given the steep topography (i.e. sudden drop-offs) and the wide prevalence of rocky substrata, the distribution of *P. oceanica* meadows in the study area appeared to be primarily driven by geomorphology. *P. oceanica* meadows were naturally restricted to depths between 5 m and 22 m and presented a rather patchy distribution. The only exception was the relatively shallow underwater ridge connecting Akrotiri Cape to Aspronisi Island, where milder slopes enabled the development of more extensive and slightly deeper meadows (maximum depth of 25 m).

Overall, 8 suitable sampling sites (i.e. extensive meadows at 15 m depth) were selected within the wider study area. Mean values (\pm SE) of each metric as estimated per site are summarized in Table 2. All meadows studied were dense (shoot density = 461 ± 45.11 shoots m⁻²) and presented a *good* conservation status (Conservation Index, CI = 0.89 ± 0.02). Their overall vitality was invariably evaluated as *good* (Table 2).

Data analysis indicated statistically significant differences among stations for all metrics (meadow cover: H = 7.626, p < 0.001; shoot density: F = 10.389, p < 0.001; plagiotropic growth of rhizomes: H = 15.753, p = 0.027), except for the CI (H = 7.095, p = 0.419) (Fig. 3). *Post-hoc* analysis revealed a possible differentiation pattern for the stations, based on their spatial distribution, only as regards shoot density and percentage of plagiotropic growth of rhizomes (Fig. 3). More specifically, highest shoot density and lowest percentages of plagiotropic growth of rhizomes were detected at sites located along the southern coasts of Akrotiri Peninsula (Table 2; Fig. 3).

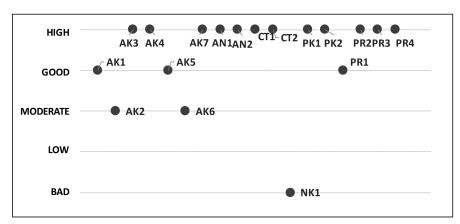


Fig. 2: Ecological status categories as determined per site according to the Ecological Evaluation Index.

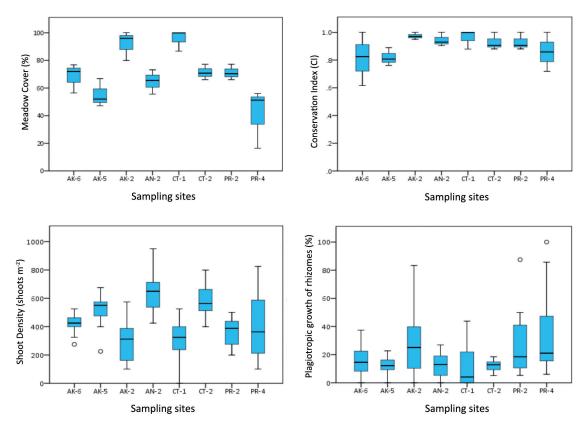


Fig. 3: Boxplots depicting spatial variability of *Posidonia oceanica* metrics among the studied sites. Boxes and whiskers represent within site variability.

Integrated assessment of fish and benthic assemblages

A. Infralittoral fish communities

We counted and estimated the length of 14,659 fish specimens belonging to 38 species and 16 families. Another 5 families (Mugilidae, Atherinidae, Blennidae, Gobiidae and Tripterygiidae) were recorded but not identified to species level. The most abundant family was the Pomacentridae consisting of the single species Chromis chromis, while the families with most species were the Labridae (9 species) and the Sparidae (8 species). The vast majority of fish encountered (81% at 5 m depth and 68% at 15 m depth) belonged to 0-5 and 5-10 cm size classes. Accordingly, most individuals of commercially exploited species recorded were juveniles (Fig. S1–S8). At 5 m depth, total fish biomass presented a mean value (\pm SE) of 7.96 \pm 2.14 g m⁻² across rocky sites, and 11.4 ± 4.35 g m⁻² across sites with P. oceanica meadows (Fig. 4A). At 15 m depth, the mean value of total biomass was 10.6 ± 2.41 g m⁻² across rocky sites, and 12.7 ± 2.79 g m⁻² across sites with *P. oce*anica meadows (Fig. 4D). Total biomass between 5 m and 15 m did not differ significantly (Kruskal-Wallis test, p > 0.05). However, the biomass corresponding to the different trophic groups differed between the two depths (Table 3). At 5 m depth, herbivores accounted for the largest proportion of total biomass at most sites, whereas at 15 m depth zooplanktivores were the predominant trophic group. At both depths, apex predators represented a very

small proportion – as only few small-sized individuals were encountered (Fig. S5) – and were totally absent at half of the sampling sites. Three alien fish species, all of Red Sea origin, were recorded during the visual surveys: the dusky spinefoot *Siganus luridus*, the marbled spinefoot *Siganus rivulatus*, and the bluespotted cornet fish *Fistularia commersonii*. At 5 m depth, the siganids accounted for 82% of herbivorous fish biomass and 44% of total fish biomass. At 15 m depth, the siganids accounted for 74% of herbivorous fish biomass and 14% of total fish biomass. Most siganids encountered belonged to the 10-15 cm size class (Fig. S9 and S10).

B. Structure and composition of benthic communities

Rocky infralittoral sites at 5 m depth exhibited benthic communities mainly dominated by turf algae (mean cover \pm SE: 61.4 \pm 19.6%), followed by calcified algae (14.7 \pm 11.4%). Bare rock was also found to be common within quadrats with a mean cover of 9 \pm 7.3%. On the

Table 3. Results of Kruskal-Wallis test on differences in fish group biomass between sites at 5 m and 15 m depth.

Fish group	Chi-squared	df	p-value
Zooplanktivores	6.52	1	0.010
Herbivores	7.6237	1	0.005
Carnivores	1.9048	1	0.167
Apex predators	3.5363	1	0.060

other hand, the canopy layer, which usually characterizes pristine Mediterranean shores, was found to be greatly reduced (6.7 \pm 7.9%), consisting of only a few *Cystoseira* species (mainly C. spinosa, but also C. corniculata, C. elegans and C. foeniculacea f. tenuiramosa). The bushy layer (including Padina pavonica, Halopteris scoparia, Codium bursa, Dictyopteris polypodioides, Gelidium bipectinatum) was also poor, with a mean cover not exceeding 6.3 \pm 9.4%, while the respective values for epiphytes and invertebrates (mainly sponges and bivalves) (Fig. 4C) were even lower (<2%). The benthic structure and composition at 15 m depth, where turf algae were also dominant (62.1 \pm 16.2%) (Fig. 4F), followed by calcified algae and bare rock (12.7 \pm 8.1% and 10.5 \pm 5.5% respectively) was quite similar. Again, the canopy and bushy layers were poor (5.5 \pm 8.1% and 7.6 \pm 4.4% respectively), while invertebrates and epiphytes presented low values (<1.3%). Overall, no statistically significant differences were observed between the cover of benthic communities at 5 m and 15 m depth (Kruskal-Wallis test, p > 0.05).

C. Sea urchin biomass

Two species of sea urchin were encountered, namely *Paracentrotus lividus* and *Arbacia lixula*. The density and biomass of sea urchins were found to be very low at both depths. At 5 m depth, sea urchins were recorded at half of the studied sites (Fig. 4B), with total biomass ranging between 13.6 and 267.6 gr m⁻², and a mean value (\pm SE) of 61.6 \pm 26.8 gr m⁻². At 15 m depth, only few juvenile sea urchins (<2 cm) of the species *A. lixula* were recorded at only one station where total biomass was 8.07 gr m⁻² (Fig. 4E).

D. Relationships between fish and benthic assemblages

No significant relationships were detected between total fish biomass or fish carnivore biomass and sea urchin biomass across sites. Furthermore, no significant relationship was detected between sea urchin and *Diplodus* spp. biomass, which are the main predators of adult sea urchins. At 5 m depth, a positive relationship between herbivore fish and bare rock ($r_s = 0.563$, p = 0.02) was revealed, whereas negative relationships were detected between canopy algae and herbivorous fish ($r_s = -0.486$, p = 0.05), as well as with sea urchins ($r_s = -0.505$, p = 0.04).

Other species of interest

A total of 92 macrobenthic invertebrate species were recorded throughout our study area belonging to 9 higher taxa (Table 4). The list includes 12 species that are protected by international regulations and conventions, 11 species of commercial interest whose harvesting is regulated by national regulations and international laws, and two alien species.

Conspicuous benthic invertebrates that were consistently recorded throughout the entire study area were the sponges *Crambe crambe, Spirastrella cunctatrix, Age*-

las oroides, Petrosia ficiformis, Chondrosia reniformis and Sarcotragus foetidus, the bryozoans Schizoporella cf. dunkeri and Reptadeonella violacea, the nudibranch Peltodoris atromaculata (always associated with P. ficiformis sponges), the ascidian Halocynthia papillosa and the bivalve Spondylus gaederopus. Other relatively common species of conservation interest were the bivalve Pinna nobilis, sponges of the genus Axinella (mainly A. polypoides), the brown cowry (Luria lurida) and the scleractinians Balanophyllia europaea and Madracis pharensis. The finding of several dead shells of Triton's trumpet (Charonia variegata) also indicates the presence of this otherwise elusive – due to its mostly nocturnal habits – protected species. With regard to alien invertebrates, only the sub-tropical crab *Percnon gibbesi* was commonly encountered, exclusively at stations within the Caldera. The bivalve Pinctada imbricata radiata was found at only one site of the Perissa Rock, while a couple of dead shells of the gastropod Conomurex persicus suggest potential presence of live specimens as well.

A comprehensive inventory of all species recorded at each site (0-1 m, 5 m and 15 m observations integrated) is given in Table 5.

Discussion

Good environmental quality conditions were found to characterize the upper infralittoral rocks of southern Santorini Island, as reflected in rich late successional algal communities dominated by *Cystoseira* species. Both sheltered and exposed shallow rocky coasts along Akrotiri Peninsula, Perissa Rock and the islets of Caldera were assessed as presenting a *good* to *high* ecological status according to the EEI scale. Few exceptions were detected, among which the striking case of the southern coast of Nea Kameni Islet where few *r-selected* species (mainly turf algae and species of the *Laurencia* complex) practically monopolized the rocky substratum, a sharp contrast to the lavish algal communities that once thrived here under the effect of volcanic seeps (authors' personal observations, 2007).

Table 4. Number of benthic invertebrate species recorded across sites (Total, Protected, Commercially Important and Alien).

Higher taxa	Total Number	Protected	Commercial	Alien
Foraminifera	1			
Porifera	27	4		
Cnidaria	8	4		
Annelida	4			
Mollusca	23	3	9	2
Crustacea	2			1
Bryozoa	7			
Echinodermata	12	1	1	
Tunicata	8		1	
Sum	92	12	11	3

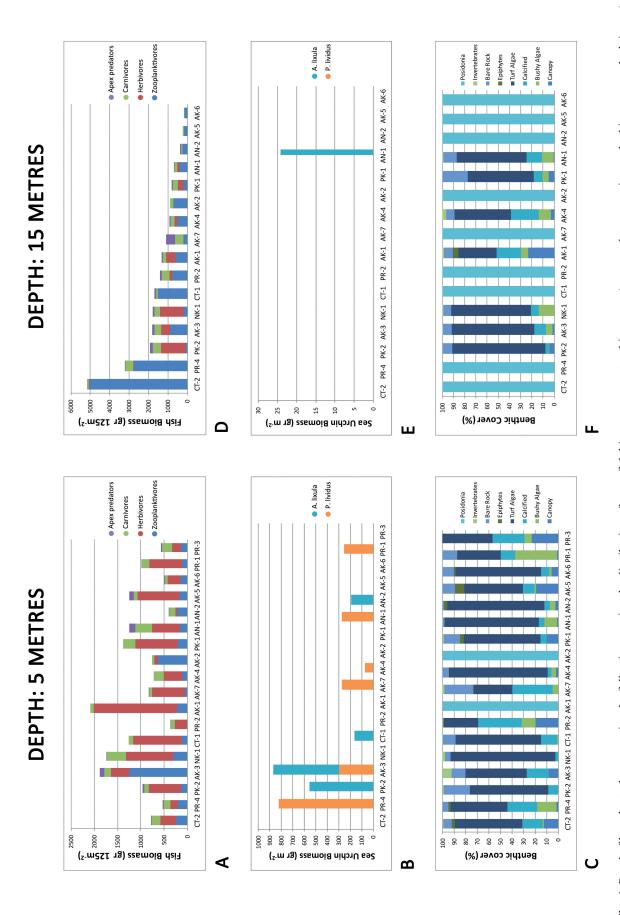


Fig. 4: Panel of bar-charts demonstrating the following per site: the distribution of mean fish biomass among trophic groups (apex predators, carnivores, herbivores, zooplanktivores) at A) 5 m and D) 15 m; the mean sea urchin (Paracentrotus lividus and Arbacia lixula) biomass at B) 5 m and E) 15 m; and the mean percentage cover of benthic layers: Posidonia oceanica, invertebrates, bare rock, epiphytes, turf algae, calcified algae, bushy algae and canopy algae at C) 5 m and F) 15 m respectively.

(continued)

Table 5. Presence of invertebrate species recorded per site (all studied depths summarized), and their respective information on conservation or other interest. "Status" details are given below.

Post part					Per	Perissa Rock Sites	k Sites			Akrot	Akrotiri Peninsula	sula				Ü	Control Sites	Sites		
Partial Part	Phylum	Species	Authority	Status															AN1	AN2
Automatic acution Sebartic 1862 Separtic	FORAMINIFERA																			
Material State Statistic 1862 Statistic 1864 Stat	Foraminifera	Miniacina miniacea	Pallas, 1766						+			+								+
Activación contact Schmidt, 1862 Activación contact de la	PORIFERA																			
Apprised consists Schmidt, 1864 Sept.	Porifera	Acanthella acuta	Schmidt, 1862					+		+	+					+	+		+	+
Advision analysisky by March 1833 1111 A strategia contaction of Sebarati, 1842 1794 1711 A strategia contaction of Sebarati, 1842 1794 1711 A strategia contaction of Sebarati, 1842 1794 1711 A strategia contaction of Sebarati, 1842 1794 1794 1794 1794 1794 1794 1794 1794	Porifera	Agelas oroides	Schmidt, 1864		+		+	+	+	+	+				+	+	+	+	+	
Atmosited connotation Espect 1794 111.21 +	Porifera	Aplysina aerophoba	Nardo, 1833	1/11				+		+	+	+		+					+	
Assingly amendonicy Sept. 1794 Asingly beloaded Septimid. 1862 Asingly reaccessis Rises, 1836 Cloudroise colored Colored Septimid. 1862 Cloudroise colored Colored Septimid. 1862 Cloudroise colored Colored Septimid. 1893 Cloudroise colored Colored Colored Septimid. 1893 Cloudroise colored Colored Colored Septimid. 1893 Holling are placed Colored	Porifera	Axinella cannabina	Esper, 1794	1/11							+								+	
Assingly polygoides Statistical States 111; 211	Porifera	Axinella damicornis	Esper, 1794							+	+		+						+	
Chandre transcoores Espect 1794 Chandre flat revolved revolved Chandre flat around Chandre flat arou	Porifera	Axinella polypoides	Schmidt, 1862	1/II; 2/II				+	+		+		+			+	+		+	
Clipatria tistation of the control o	Porifera	Axinella verucosa	Esper, 1794																+	
Chandralia mercula Chandra	Porifera	Calyx nicaeensis	Risso, 1826								+			+				+	+	
Clouderstare readjorminks Naticle 1847	Porifera	Chondrilla nucula	Schmidt, 1862								+			+				+	+	+
Cliona Sp. Cliona Sp. Cliona Sp. Cliona Sp. Cliona Sp. Cliona Coloura Colo	Porifera	Chondrosia reniformis	Nardo, 1847		+	+				+	+	+	+			+	+	+	+	+
Clione celate Crimit 1825 Fig. Fig	Porifera	Cliona sp.					+										+			
Claima of paramenia Corriero & Scalaria Listo.] Paramenia Corriero & Scalaria Listo.] Paramenia Parame	Porifera	Cliona celata	Grant, 1826					+			+									
Cliona syridis Schmidt, 1862 Schmidt, 1862 Schmidt, 1862 Schmidt, 1863 Schmidt, 1863 Schmidt, 1864 Schmidt, 1865 Schmidt, 18	Porifera	Cliona cf. parenzani	Corriero & Scalera-Liaci, 1997		+															
Crambe crambe Schmidt, 1862 Schmidt, 1860 Schmidt, 1880 Schmidt, 1884 Schmidt, 1864 Schmidt, 1862 Schmidt, 1863 Schmidt, 1862 Schmidt, 1863 Schmidt, 1862 Schmidt, 1863 Schmidt, 1864 Schmidt, 186	Porifera	Cliona viridis	Schmidt, 1862						+							+		+	+	
Pictornella incisca Schmidt, 1880 Authorised Schmidt, 1880 Authorised solumella incisca sp. Authorise sp. Authorise survivals Authorise su	Porifera	Crambe crambe	Schmidt, 1862			+	+	+		+	+	+		+		+	+	+	+	
Heminycale columella Boverbank, 1874 Heminycale columella Boverbank, 1874 Heminycale columella Boverbank, 1864 Herinia ovos Schmidt, 1864 Herinia ovos Schmidt, 1864 Herinia ovos Schmidt, 1864 Herinia ovos Schmidt, 1865 Horberto congruentia concerne Schmidt, 1865 Horberto columella Boverbank, 1866 Horberto condycale columella Schmidt, 1862 Horberto columella Schmidt, 1862 Horberto columella Schmidt, 1863 Horberto columella Charleston Schmidt, 1864 Horber	Porifera	Dictyonella incisa	Schmidt, 1880								+					+		+	+	
Hemimycale colume Ia Bowerbank, 1874 Hemimycale colume Ia He	Porifera	Haliclona sp.							+											
Herita spp. Herita oves Schmidt, 1864 Herita oves Schmidt, 1862 Herita oves Schmidt, 1864 Herita over Herita over Herita over Schmidt, 1864 Herita over Herita over Herita over Herita over Schmidt, 1864 Herita over Herit	Porifera	Hemimycale columella	Bowerbank, 1874								+				+					
Printa oros Schmidt, 1864 Peirotia oros Schmidt, 1862 Peirotia oros Schmidt, 1862 Peirotia oros	Porifera	Ircinia spp.								+	+							+	+	
Petroia variability Sebmidit, 1862 + <	Porifera	Ircinia oros	Schmidt, 1864							+	+								+	
Petrosia fictionnis Pointe, 1789 + <th< td=""><td>Porifera</td><td>Ircinia variabilis</td><td>Schmidt, 1862</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>+</td><td></td><td></td><td></td><td></td><td>+</td><td></td><td></td><td>+</td><td></td></th<>	Porifera	Ircinia variabilis	Schmidt, 1862								+					+			+	
Phorbas fictitius Bowerbank, 1866 + <t< td=""><td>Porifera</td><td>Petrosia ficiformis</td><td>Poiret, 1789</td><td></td><td>+</td><td>+</td><td>Т</td><td></td><td>+</td><td>+</td><td>+</td><td>+</td><td>+</td><td></td><td>+</td><td>+</td><td>+</td><td>+</td><td>+</td><td></td></t<>	Porifera	Petrosia ficiformis	Poiret, 1789		+	+	Т		+	+	+	+	+		+	+	+	+	+	
Phorbas tenacion Topsent, 1925 1/II + <t< td=""><td>Porifera</td><td>Phorbas fictitius</td><td>Bowerbank, 1866</td><td></td><td>+</td><td></td><td>+</td><td></td><td></td><td>+</td><td>+</td><td></td><td></td><td></td><td>+</td><td></td><td></td><td></td><td></td><td>+</td></t<>	Porifera	Phorbas fictitius	Bowerbank, 1866		+		+			+	+				+					+
Porifera unid. Scalarisyongias scalaris Schmidt, 1862 Schmidt, 1862 Schmidt, 1863 Schmidt, 1863 Schmidt, 1864 Schmidt, 1865 Schmidt, 1868 Annonnia viridis Balanophyllia europaea Risso, 1826 All; 5/DD Cerianthus membranaceous Schmidt, 1863 All Schmidt, 1864 Schmidt, 1864 Schmidt, 1865 H H H H H H H H H H H H H	Porifera	Phorbas tenacior	Topsent, 1925															+		
Scalarispongia scalaris Schmidt, 1862 Julia Harmonia virialis Schmidt, 1862 Harmonia virialis Schmidt, 1862 Harmonia virialis Scalarispongia scalaris Schmidt, 1863 Harmonia virialis Schmidt, 1868 Harmonia virialis Schmidt, 1868 Harmonia virialis Schmidt, 1868 Harmonia virialis Harmonia viria	Porifera	Porifera unid.											+		+	+	+	+	+	
Scalarispongia scalaris Schmidt, 1862	Porifera	Sarcotragus foetidus	Schmidt, 1862	1/II	+	+	Т			+	+	+			+		+	+		
81A Anemoria viridis Forskål, 1775 + <th< td=""><td>Porifera</td><td>Scalarispongia scalaris</td><td>Schmidt, 1862</td><td></td><td>+</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>+</td><td></td><td></td><td></td></th<>	Porifera	Scalarispongia scalaris	Schmidt, 1862		+												+			
Anemonia viridis Forskil, 1775 Anemonia viridis Esso, 1826 A/II; S/DD + + + + + + + + + + + + + + + + + +	Porifera	Spirastrella cunctatrix	Schmidt, 1868		+					+	+	+				+	+	+	+	+
Anemonia viridis Forskål, 1775 Balanophyllia europaea Risso, 1826 4/II; 5/DD + + + + + + + + + + + + + + + + + +	CNIDARIA																			
Balanophyllia europaeaRisso, 18264/II; 5/DD++	Cnidaria	Anemonia viridis	Forskål, 1775						+			+								
Condylactis aurantiaca Delle Chiaje, 1825 + +	Cnidaria	Balanophyllia europaea	Risso, 1826	4/II; 5/DD								+	+		+	+	+	+		
Condylactis aurantiaca Delle Chiaje, 1825	Cnidaria	Cerianthus membranaceous	Spallanzani, 1784				Т													
	Cnidaria	Condylactis aurantiaca	Delle Chiaje, 1825				+					+								

Phylum	Crosice	Authority	Stotue	PP.1	rissa Ko PD2	Ferissa Kock Sites	es PB4 AK1	K1 AK2		AKrotiri Peninsula AK3 AK4 AK5	umsula AK5	AKG	A K7	£	CL	Contr PK1 P	Control Sites	5	×	NA NA
L mynum	Species	Authority	Status	- 1	ł			-		- 1	- 1	OWE	A C			- 1	- 1			7
Cnidaria	Eudendrium spp.						г	+	+											
Cnidaria	Leptopsammia pruvoti	Lacaze-Duthiers, 1897	П/4				т	+		+									+	
Cnidaria	Madracis pharensis	Heller, 1868	4/II; 5/LC		+					+			+			+	+	+	+	
Cnidaria	Polycyathus muellerae	Abel, 1959	4/II							+			+							
Chidaria	Scleractinia unid.																	+		
ANNELIDA																				
Annelida	Hermodice carunculata	Pallas, 1766		+			+	+				+						+		+
Annelida	Protula sp.															+				
Annelida	Sabella spallanzanii	Gmelin, 1791					+	_	+											
Annelida	Serpulidae spp.			+		+	Т	+	+		+					+	+	+	+	
MOLLUSCA																				
Mollusca	Bittium sp.															+				
Mollusca	Bolma rugosa	Linnaeus, 1767	6				т	+								+	+	+		
Mollusca	Cerithium sp.					+				+										
Mollusca	Hexaplex trunculus	Linnaeus, 1758																+	+	
Mollusca	Elysia timida	Risso, 1818							+							+				
Mollusca	Felimare picta	Schultz in Philippi, 1836						+												
Mollusca	Luria lurida	Linnaeus, 1758	1/II; 2/II; 6; 9						+	+				+		+				
Mollusca	Octopus vulgaris	Cuvier, 1797	6	+															+	+
Mollusca	Pecten sp.																			+
Mollusca	Peltodoris atromaculata	Bergh, 1880		+			+	+	+	+			+			+	+	+	+	
Mollusca	Pinctada imbricata radiata	Leach, 1814	9;10		+															
Mollusca	Pinna nobilis	Linnaeus, 1758	1/II; 2/II; 3/ IV; 6;7;8;9				+	+						+						
Mollusca	Pinna rudis	Linnaeus, 1758						+			+	+						+		+
Mollusca	Sepia officinalis	Linnaeus, 1758	6																+	
Mollusca	Thylacodes arenarius	Linnaeus, 1758				+									+		+			+
Mollusca	Spondylus gaederopus	Linnaeus, 1758	7;8;9	+	+		+	+	+			+				+	+	+	+	+
Mollusca	Thuridilla hopei	Vérany, 1853			+															
Mollusca	Umbraculum umbraculum	Lightfoot, 1786																	+	
Mollusca	Vermetidae spp.	(Roth) C.Agardh, 1823								+	+			+		+	+	+	+	
CRUSTACEA																				
Crustacea	Paguridae spp.					+	+			+		+				+	+	+	+	
Crustacea	Percnon gibbesi	H. Milne-Edwards, 1853	10									+		+			+			
BRYOZOA																				
Bryozoa	Bryozoa unid.							+												
Bryozoa	Margaretta cereoides	Ellis & Solander, 1786						+			+		+	+						+
Bryozoa	Myriapora truncata	Pallas, 1766							+							+	+	+	+	

Table 5 (continued)

Table 5 (continued)

				Dog	ises D	Dowiego Dooly Citor			-	l initia	A Irnotini Doningulo	ا					Control Citos	3400		
Phylum	Species	Authority	Status	PRI	PR4	PR3	P.4	AK1 AK2		14	AK4 AK5	9 VK &	AK7	L	C L $^{\circ}$	۵	DEC DEC	NK1	NA	VNA CNA
ı ııyıdını	smade	Sa tomas	Status								- 1						- 1			7
Bryozoa	Reptadeonella violacea	Johnston, 1847			+	+			+	+	+	+	+	+	+	+	+	+	+	+
Bryozoa	Rhynchozoon neapolitanum	Gautier, 1962			+	+				+						+				
Bryozoa	Schizomavella mamillata	Hincks, 1880			+								+							
Bryozoa	Sertella sp.							+			+									+
Bryozoa	Schizoporella cf. dunkeri	Reuss, 1848			+	+			+	+	+	+	+	+	+	+	+	+	+	+
ECHINODERMATA	_																			
Echinodermata	Amphiura filiformis	O.F. Müller, 1776															+	+		
Echinodermata	Arbacia lixula	Linnaeus, 1758		+				+				+		+						
Echinodermata	Coscinasterias tenuispina	Lamarck, 1816														+				+
Echinodermata	Echinaster sepositus	Retzius, 1783						+												
Echinodermata	Hacelia attenuata	Gray, 1840																+		
Echinodermata	Holothuridae unid.								+											
Echinodermata	Holothuria forskali	Delle Chiaje, 1823					+													
Echinodermata	Holothuria sanctori	Delle Chiaje, 1824														+				
Echinodermata	Marthasterias glacialis	Linnaeus, 1758																+		
Echinodermata	Ophidiaster ophidianus	Lamarck, 1816	1/II; 2/II				+		+											
Echinodermata	Paracentrotus lividus	Lamarck, 1816	6	+					+	+	+		+							
Echinodermata	Sphaerechinus granularis	Linnaeus, 1758																+		
TUNICATA																				
Tunicata	Aplidium elegans	(Giard, 1872)														+				
Tunicata	Clavelina sp.									+										
Tunicata	Didemnidae spp.			+																
Tunicata	Didemnum maculosum	(Milne-Edwards, 1841)												+						
Tunicata	Diplosoma spongiforme	Giard, 1872														+				
Tunicata	Microcosmus spp.															+				
Tunicata	Microcosmus sabatieri	Roule, 1885	6														+	+	+	
Tunicata	Polysyncraton lacazei	Giard, 1872																		+
DEAD SHELLS																				
Mollusca	Conomurex persicus	Swainson, 1821	10													+				
Mollusca	Luria lurida	Linnaeus, 1758	1/II; 2/II; 6; 9														+			+
Mollusca	Ostrea sp.		6; 9															+		
Mollusca	Spondylus gaederopus	Linnaeus, 1758	7; 8; 9							+						+		+		
Mollusca	Semicassis granulata	Born, 1778				+														
Mollusca	Charonia tritonis variegata	Lamarck, 1816	1/II; 2/II; 9					+						+						+
	# # # # # # # # # # # # # # # # # # #							;			,	7	;	ľ	l	١,	,			,

European wildlife and natural habitats; 3. Habitats Directive 92/43/EEC; 4. CITES - Convention on International Trade in Endangered Species of Wild Fauna and Flora, 1973; 5. Red List of IUCN - the International Union of Conservation of Nature; 6. Presidential Decree 67/1981; 7. Presidential Decree 109/2002; 8. Presidential Decree 227/200; 9. Exploited Spe-1. Barcelona Convention - Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean; 2. Bern Convention - Convention on the conservation of cies; 10. Alien (non indigenous) species; I, II, III, IV. Appendix/Annex I, II, III, IV, DD. Data deficient; LC. Least Concern These exceptions, however, are not clearly associated with coastal sources of nutrient enrichment and likely reflect strictly localized or seasonal stresses that should be regarded as outliers to an otherwise healthy ecosystem component.

Similarly, healthy ecological conditions were reflected in the adjacent *P. oceanica* meadows, which have been studied for the first time so thoroughly in the Cyclades Archipelago. Critical evaluation of the applied set of metrics revealed that the meadows of Santorini are still in equilibrium and present a good vitality status. Slight deviations from reference conditions were detected, such as the comparatively lower shoot densities recorded at a few sites along the Akrotiri Peninsula, which may be related to more intense pressures exerted here by recreational activities, i.e. boat anchoring and mooring. Even in these cases, however, meadows were observed to respond positively through increased plagiotropic rhizome growth (Francour *et al.*, 1999).

Both evaluation approaches described above, are in agreement with the *high* ecological status that has been assessed through the application of the BENTIX biotic index on soft bottom zoobenthic communities of previous monitoring studies conducted in Santorini Caldera (HCMR, 2011; 2012) that adequately express an oligotrophic area, largely unaffected by either organic or inorganic pollutants (HCMR, 2007-2012).

However, the case of fish and rocky infralittoral benthic communities is more alarming. Notably, fish biomass displayed very low values in the study area as compared to other parts of the Mediterranean, a result that is consistent with a previous study in the wider Cyclades region (Giakoumi et al., 2012). Apex predators, in particular, were encountered in low numbers and small sizes at most sites, or were totally absent at several others. In contrast, pristine areas and well-enforced marine reserves are characterised by a dominance of top predators in terms of total fish biomass, presenting an inverted (top-heavy) biomass pyramid (DeMartini et al., 2008; Sandin et al., 2008). In such pristine habitats, an increase in total fish biomass has been documented, mostly characterised by a greater increase in apex predator biomass (Sandin et al., 2008). In that light, the low apex predator biomass that was invariably recorded in the study area, indicates a depleted coastal fish community.

This conclusion is further supported by the fact that the vast majority of commercially exploitable specimens encountered were juveniles (Fig. S1-S8).

The predominant presence of two invasive herbivore fishes, i.e. *S. luridus* and *S. rivulatus*, was remarkable. During the study period (October 2012), large schools of these species thrived in the waters of Santorini, whereas during field surveys conducted in July 2008 only *S. luridus* had been recorded (Giakoumi, 2014). This recent introduction of *S. rivulatus* must have increased grazing pressure in the area. Both these lessepsian species are capable of significantly altering the structure and composi-

tion of the infralittoral marine vegetation in the Mediterranean (Sala *et al.*, 2011; Giakoumi, 2014), and thus their overabundant populations in the study area pose a direct threat to its native algal communities.

Indeed, the infralittoral vegetation at both 5 m and 15 m depth was mainly characterized by turf algae, various calcified species and the ubiquitous presence of bare rock. On the contrary, the perennial canopy algae of the order Fucales – widely recognized as the main component of the shallow pristine Aegean (e.g. Montesanto & Panayotidis, 2001) and Caldera rocky coasts in particular (HCMR, 2007; 2008) – were only barely recorded during this study. Likewise, the cover of bushy algae, epiphytes and benthic invertebrates was low.

This type of phycocommunity seems to reflect the effects of fish overgrazing (Sala et al., 2011), to which turf algae are able to resist by virtue of their decumbent forms, rapid development and short life cycles, while calcified algae by virtue of their hard and rigid thalli. Canopy and bushy algae, on the other hand, are particularly prone to fish overgrazing since their palatable massive fronds readily attract herbivorous species. These observations were confirmed by the statistically significant negative relationship observed between herbivore fishes and canopy algae, and the positive relationship of herbivorous fishes and bare rock. Furthermore, the persistent dominance of canopy algae (Cystoseira spp. and, to a lesser degree, Sargassum sp.) in the upper infralittoral zone (0-1 m) is yet another indication that their scarcity in deeper habitats is a result of overgrazing; indeed, the upper infralittoral communities are too exposed to water movement and other risks (e.g. seabird predation) for most fish to use as safe foraging grounds.

Sea urchins have been traditionally regarded as keystone grazers influencing the structure and distribution of Mediterranean infralittoral macroalgal communities (e.g. Sala et al., 1998; Bulleri et al., 1999). When present in high densities, sea urchin grazing pressure may lead to complete depletion of macroalgal forests and the creation of extensive barren rocks mostly dominated by encrusting red algae (Sala et al., 1998; Guidetti & Sala, 2007). In our study area, sea urchin abundance and biomass were found to be particularly low compared to other areas of the Cyclades Islands and the Mediterranean Sea (Giakoumi et al., 2012, and references therein). In fact, most of the individuals recorded were juveniles. However, a statistically significant negative relationship was found between sea urchin biomass and canopy algal cover. Thus, while it is likely that herbivorous fishes are protagonists in forming the marine vegetation along the coasts of Santorini Island, synergistic effects from sea urchin grazing may still occur.

Most coastal sites studied along Perissa Rock, Akrotiri Peninsula and the adjacent islets were found to comprise a rich variety of habitats and benthic invertebrates, especially within the volcanic caldera, where the much steeper and more complex topography (Nomikou *et al.*, 2014) accounted for higher heterogeneity at relatively small scales.

Besides the great number of siganids and their overgrazing effects, other alien species recorded (i.e. the green alga *C. cylindracea*, the red alga *Ganonema farinosum*, the crab *P. gibbesi*, and the trumpet fish *F. commersoni*) were only occasional findings. However, on the positive side, the persistent brown algae canopies on the upper infralittoral rocky shores, as well as the presence of several juveniles of the apex predator *Epinephelus marginatus* suggest the area's potential for ecosystem recovery once a fully protected area is established and appropriate management measures are implemented.

Overall, notwithstanding minor variations among sites, our study area was assessed as undisturbed by anthropogenic pollution, but highly disturbed by the combined pressures of long-term overfishing and excess herbivory by the increasing populations of invasive fish species. The establishment of an MPA is likely to enhance ecosystem recovery by stimulating the recovery of the functional role of top predators, and especially large groupers, which are known to prey on siganids in the Eastern Mediterranean (Aronov & Goren, 2008). Given, however, the strong alterations in ecosystem structure, the establishment of the MPA will have to be accompanied by early restoration actions targeting the decrease (and if possible removal) of invasive species. Therefore, priority should be given to management measures for the regulation of the two herbivore fishes that have led to severe deforestation of the infralittoral rocky shores of Santorini Island, as well as other locations in the southern Aegean Sea (Bianchi et al., 2014; Vergés et al., 2014; authors' unpublished data).

The involvement of key stakeholders throughout the MPA establishment process in Santorini is pivotal in reinforcing compliance and success. Several public discussion events and consultation meetings have been organized thus far aiming to inform local authorities and the general public, to achieve consensus for protection and, more importantly, to enhance active engagement in the planning process. Taking into account both ecological (as highlighted in this study) and socioeconomic requirements (as later expressed by various key stakeholders), there is now general agreement and common interest in the establishment of an MPA along a ~9.8 km coastal stretch of Akrotiri Peninsula (~4.21 km²). This is a slow, ongoing process mostly due to labyrinthine bureaucratic and legislative issues, which nevertheless allows adequate time for the local community to adjust to this novel perspective.

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Appendix

Table 1. List of the *Posidonia oceanica* (editor's choice) metrics studied, anticipated responses to different impacts, and sampling protocols.

Metrics	Impact or stress	Expected Response	Method
Meadow Cover (%)	Reduction of light availability. Burial. Direct elimination due to trawl fishing, boat anchoring, coastal construction, etc.	Vegetal cover decrease	Estimated by the non-destructive Line Intercept Transect (LIT) methodology (Montefalcone <i>et al.</i> , 2007) along three transect lines of 25 m placed in three random directions. The observer recorded the intercept to the nearest centimetre corresponding to the point where the key attributes (e.g. <i>Posidonia</i> bed, sandy bottom, dead matte, etc.) changed under the line. Meadow Cover (R%) is calculated using the following formula: $R\% = \Sigma(Lx/25 \times 100)$; where the length of each key attribute (Lx) is the distance between two recorded intercepts at each LIT and is calculated by subtraction.
Shoot density (shoots m ⁻²)	Reduction of light availability. Burial. Direct elimination due to trawl fishing, boat anchoring, coastal construction, etc.	Shoot mortality (Shoot density decrease)	Shoot number was counted in $20 (20 \times 20 \text{ cm})$ replicate quadrats randomly set along the three replicate line transects at 15 m depth (4 quadrats per transect) (Boudouresque <i>et al.</i> , 2006).
Plagiotropic growth of rhizomes (%)	Reduction of light availability. Sediment resuspension. Burial. Boat anchoring, coastal construction, etc.	Increase of the percentage of plagiotropic rhizomes	In situ observation of plagiotropic rhizomes in the same 20 replicate quadrats (20×20 cm) used for shoot density (Boudouresque <i>et al.</i> , 2006).
Lower Limit Typology	Reduction of light availability. Burial. Direct elimination due to trawl fishing, boat anchoring, coastal construction, etc.	Change to different type of LL	In situ observation of the presence of dead <i>P. oce-anica</i> shoots (dead matte) and plagiotropic rhizomes over the LL. Five types of the LL have been described (progressive, erosive, sharp, sparse and regressive) (Pergent <i>et al.</i> , 1995). *
Conservation Index (CI)	Reduction of light availability. Burial. Direct elimination due to trawl fishing, boat anchoring, coastal construction, etc.	Decrease to lower values	Calculation of the CI applied to data obtained using the LIT method, using the following formula: $CI = P / (P + D)$, where P is the % cover of living P. oceanica plants and D is the % cover of dead matte (Montefalcone, 2009).

^{*} The results of the LL typology were assigned to five status categories: progressive and erosive (P) = high, sharp high cover (S+) = good, sharp low cover (S-) = moderate, sparse = poor status, regressive = bad status) (Pergent *et al.*, 2015).

Table 2. Assessment of the vitality of *Posidonia oceanica* meadows, based on the applied set of metrics (UNEP/MAP-RAC/SPA, 2011, modified).

Metric	High (5)	Good (4)	Normal (3)	Poor (2)	Bad (1)
Shoot density (shoots m ⁻²)	>492	492-372	372-253	253-134	<134
Plagiotropic growth of rhizomes (%)	-	-	< 30	30-70	>70
Lower Limit Typology	Progressive / Erosive	Sharp+	Sharp-	Sparse	Regressive
Conservation Index	> 0.9	0.9 - 0.7	0.7 - 0.5	0.5 - 0.3	< 0.3
The vitality index corresponds to the averag	e of the four metrics (r	max= 5, min= 1)	-		

Table 3. Checklist for taxa recorded at the upper infralittoral (0-1 m) rocky shores across the study area (18 sampling stations) with respective mean % cover value, standard error (\pm SE), frequency of occurrence (f), and Ecological State Group (according to Orfanidis *et al.*, 2001).

Taxa/Morphological Group	Mean	SE	f	ESG
Amphiroa rigida J.V. Lamouroux	0.011	0.008	2	I
Anadyomene stellata (Wulfen) C. Agardh	0.349	0.163	7	I
Caulerpa cylindracea Sonder	0.139	0.096	3	II
Chrysophyta	0.176	0.149	3	II
Corallina sp.	1.022	0.487	8	I
Cystoseira spp.	42.822	4.828	18	I
Dictyopteris polypodioides (De Candolle) Lamouroux	0.006	0.006	2	II
Dictyota spp.	0.017	0.009	3	II
Encrusting red algae	6.928	1.602	18	I
Flabellia petiolata (Turra) Nizamuddin	0.154	0.154	1	I
Jania spp.	18.854	2.349	18	I
Laurencia complex	6.338	2.551	11	II
Padina pavonica (Linnaeus) Thivy	0.076	0.037	8	I
Sargassum sp.	2.373	1.921	7	I
<i>Titanoderma trochanter</i> (Bory) Benhissoume, Boudouresque, Perret-Boudouresque <i>et</i> Verlaque	0.565	0.489	3	Ι
Turf Algae	20.046	2.882	18	II
Valonia sp.	0.006	0.006	1	II